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NOTES ON THE ORIGIN AND FUNCTION OF THE ARTIODACTYL TARSUS

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INTRODUCTION

Artiodactyls appear for the first time in Lower Eocene (Wasatchian) deposits. At this early stage in artiodactyl evolution, the tarsus has already developed its characteristic form, including the double-trochleated astragalus, and is certainly the most diagnostic part of the skeleton. Although other features of the skeleton also suggest reference to this order, the dentition is very difficult or impossible to distinguish from that of the hyopsodontid condylarths (Simpson, 1937).

The evolution of the astragalus from the generalized ferungulate to the artiodactyl type, accompanying changes in the calcaneum, and to a lesser extent alterations in the other tarsal elements resulted in the introduction of a basic ordinal character. Simpson (1944) has pointed out that the earliest known members of all the orders of mammals already possess most of their characters of ordinal rank. The hiatus between such primitive representatives of an order and their possible ancestors is usually great, with intermediate or transitional stages either unknown, or in some cases possibly not recognized. Hence the determination of a generalized ancestral condition and, more particularly, of the transitional stages leading to such a basic ordinal character is necessarily largely inferential, based for the most part on a few characters that appear to indicate affinity and thus tend to bridge, however incompletely, the morphological gap. Thus in the Artiodactyla, the dentition seems to be the best connecting link between this order and a group of primitive condylarths, the tarsus and other parts of the skeleton offering no definite evidence regarding ancestry.

While the ancestry of a number of the modern orders of mammals must be traced back into the Cretaceous, and the time interval involved in their origin can only be very roughly estimated, many groups, such as the Rodentia, Chiroptera, Cetacea, and the various ungulate orders, very probably had a Paleocene origin. As the Paleocene had a duration of about 15 million years, the basic ordinal characters of these latter groups presumably developed in less than that time. The apparent relatively rapid evolution of such basic ordinal characters has been discussed by Simpson (1944) and by Wright in several papers and will not be elaborated upon here.

One of the most important factors in

the section pressure affecting a pre-artiodactyl population, particularly in unforested country, would be predator pressure. As Huxley (1942) has pointed out, the development of many ungulate specializations, such as the ability to ruminate and the various modifications permitting greater speed, were undoubtedly associated with the constant presence of predatory carnivores. Under such narrowly specified environmental conditions, wide variability would not be favored, and a highly specialized mechanism such as the artiodactyl tarsus could conceivably develop in a relatively short period of time. Once a definite trend towards an advantageous morphological specialization has been initiated in a population, it is highly probable that further random mutations favoring this trend would be preserved. Other mutations, although equally favorable but leading in a somewhat different adaptational direction, would be less likely to survive.

A trend of this sort could have continued to develop under the impetus of selection pressure until the biomechanical limit of specialization was reached (Huxley, 1942), the point at which theoretically the greatest possible degree of mechanical efficiency is attained. As stated before, the basic pattern of the artiodactyl tarsus was already fully developed in the Lower Eocene, and it would appear that the biomechanical limit was practically reached at that time. This was almost certainly true of the astragalocalcaneal complex, as the morphology of these elements has been altered but little excepting for minor refinements. The more distal portion of the tarsus, in certain families, has experienced some fusion and elimination of elements resulting in greater tarsal consolidation.

Matthew was well aware of the conservatism of the astragalus within a given order of mammals and laid great stress on its importance in taxonomy, although, to the writer's knowledge, he never speculated as to the reason for its resistance to further adaptional change.

The purpose of this paper is to consider, on the basis of known evidence, the transformation of the primitive ferungulate tarsus into the artiodactyl type, with particular reference to the astragalocalcaneal complex. The accompanying functional changes are discussed together with a consideration of the mechanics of the definitive artiodactyl tarsus.

The writer is obligated to Dr. M. A. Emmerson of the School of Veterinary Medicine of the University of Pennsylvania for the roentgenograms of the hind limb of a dog, goat, and pony in different stages of dorsiflexion and to Drs. W. K. Gregory, G. G. Simpson, and E. H. Colbert for helpful advice. The illustrations were prepared by the Illustrators Corps of the American Museum.

THE PRIMITIVE FERUNGULATE TARSUS

The resemblance between the dentition of the hyopsodontid condylarths and the bunodont artiodactyls is considered by Simpson to be too great to be ascribed to convergence, and it is therefore possible that the primitive hyopsodontids represent the ancestral stock from which the artiodactyls arose. Pearson's (1927) observation of the close similarity between the mastoid region of the meniscotheriid condylarth *Pleuraspidotherium* and that of the primitive artiodactyls further supports this general hypothesis. Simpson's (1945) coining of the term Ferungulata as a cohort, including both the carnivores and ungulates, is a major step in the development of a natural classification of a greatly differentiated group with a common Paleocene origin.

From the standpoint of the tarsus alone, the hyopsodontids are certainly not so close to the primitive artiodactyls as to the arctocyonid creodonts (fig. 1A, B). This is well demonstrated by a comparison of the astragalus of the Lower Paleocene hyopsodontid *Choeroclaenus* and that of the arctocyonids *Loxolophus* and *Claenodon*. In these genera, this element is of a primitive, generalized nature with a very shallow tibial trochlea and transversely

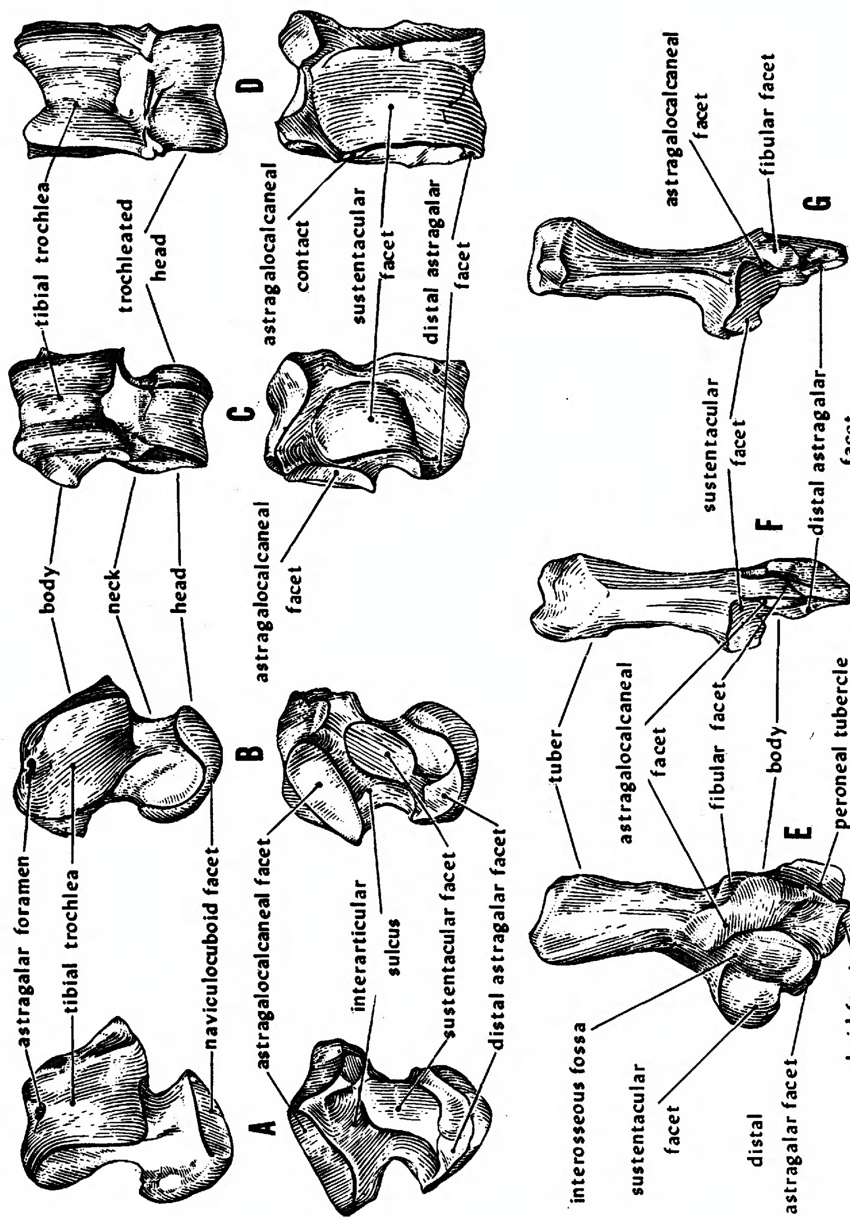

Fig. 1. Dorsal and ventral views of the astragalus and dorsal views of the calcaneum showing the morphological features discussed in the text. A, E. *Claenodon*. B. *Choeroclaenus*. C. *Diacodexis*. D, G. *Ovis*. F. *Merycochoerus*.

flattened head. In view of this basic resemblance, and the evidence offered by the dentition mentioned above, the artiodactyl tarsus could be derived validly from either the arctocyonid or the hyopsodontid type.

Matthew (1937) concluded that the non-serial or alternating tarsus, with an articulation between the astragalus and cuboid was the primitive eutherian condition, thus disagreeing with Cope's thesis (1881) that the serial tarsus of such types as *Phenacodus* represents the generalized ancestral pattern. The non-serial arrangement is characteristic of the artiodactyl tarsus and is almost without question a heritage character from the arctocyonid-hyopsodontid non-serial tarsus. In its functional significance, the tarsal pattern is undoubtedly correlated with weight distribution in the foot. In ungulates the non-serial tarsus is associated with the paraxonic foot, while there is a tendency, never quite consummated, for the mesaxonic type to be associated with the serial tarsus. Actually, in cursorial perissodactyls, the astragalocuboid contact is so small that the tarsus is functionally serial in type. This divergence in tarsal pattern must have occurred in the primitive ferungulate stock, and the resulting difference in weight distribution undoubtedly accompanied the development of the paraxonic foot in the artiodactyls and an approach to the mesaxonic type in the cursorial perissodactyls.

The primitive ferungulate astragalus is divided by a constricted neck into a proximal body and a distal head. The tibial trochlea, on the dorsal surface of the body, is very shallow, and the trochlear crests consequently are low and poorly defined. The body is oriented at an angle of about 30 degrees with a longitudinal axis passing through the neck and head.

A large astragalar foramen, extending plantarward to the interarticular sulcus, is located on the posterior surface of the trochlea. It has been stated that this foramen, or whatever passed through it, was responsible for greatly restricted movement in the upper ankle joint. The trochlear articular surface, however, extends posteriorly on both sides of the foramen, as in *Orycteropus*, which, incidentally, has a primitive ungulate-like postcranial skeleton (Colbert, 1941). The tibia covers the foramen during complete plantar flexion in the aardvark and must have done so in the primitive ferungulates. Thus the range of movement in the upper ankle joint of, for instance, *Claenodon*, formed an arc of about 75 degrees. The ontogeny of the astragalar foramen has not been worked out. In an adult *Orycteropus* dissected by the late Mr. H. C. Raven, only some connective tissue was found passing through the canal, and there is no evidence histologically of degenerated blood vessels or nervous tissue or of any clear-cut relationship with the interosseous ligament.

In dorsal aspect, the astragalar neck has no important morphological features. The head is dorsoventrally compressed and is divided into two distinct articular surfaces. The naviculocuboid facet, which is not clearly subdivided, is slightly curved both dorsoventrally and mediolaterally. The other facet, running along the median side of the neck and confluent with the naviculocuboid, is the articular surface, according to Matthew (1937), for a small ossicle which he considered to be a persistent reptilian tibiale. Although the homology of this bone might be questioned, its presence in *Claenodon* is beyond doubt, and the necessary facet is found in other arctocyonids and in *Choeroclaenus*.

On the plantar surface of the astragalus, the astragalocalcaneal facet (ectal facet of Osborn, 1890) is a narrow, concave oval area located along the lateral border of the body. The long axis of this facet is oriented at an angle of about 40 degrees with the long axis of the entire bone, and its oblique position causes it to be produced laterally at its distal end well beyond the body.

The sustentacular facet of the astragalus is mostly located on the plantar surface of the neck and is separated from the astragalocalcaneal facet by the deep interarticular sulcus. It is ovoid in shape and gently concave, with its long axis making an angle of about 15 degrees with the long axis of the entire bone.

The triangular distal astragalar facet is located on a ridge running mediodistally from the sustentacular facet and is confluent with the articular surface of the head. It is the only contact between the astragalar head and the body of the calcaneum. On the latter the distal astragalar facet is represented by a narrow transverse shelf along the dorsal border of the cuboid facet.

The calcaneum (fig. 1E) has a massive appearance when compared to the typical fissiped or ungulate type. The astragalocalcaneal facet, located at the proximal end of the calcaneal tuber, is oriented at an angle of about 30 degrees with the long axis of this bone and is tilted at about a 45-degree angle. It is roughly ovoid and is continuous with the convex fibular facet that is situated along its upper rim, facing dorsally.

The sustentaculum is separated from the astragalocalcaneal facet by the interosseus fossa, which, together with the interarticular sulcus of the astragalus, forms the sinus tarsi for the interosseous ligament. The sustentacular facet, located on the dorsal surface of the sustentaculum, is essentially round and slightly concave. It is tilted anteriorly in such a manner that the articular surface is oriented at a 30-degree angle with the longitudinal calcaneal axis.

The peroneal tubercle, located on the lateral surface just proximal to the cuboid facet, is very prominent and is grooved on its dorsal surface for the passage of the peroneus longus tendon. The cuboid facet covers almost the entire distal end of the calcaneum. It is roughly rhomboidal and slightly concave.

The more distal tarsal elements will not be discussed in detail except for the mention of several important features. The navicular and cuboid have an S-shaped articulation in proximal view, preventing any movement between them. The basin-shaped articular surface for the astragalus is rimmed by the outer edge of the navicular and the medial edge of the cuboid. The calcaneal facet of the cuboid is slightly convex, and the edges of the facet are not elevated. There is a well-defined groove on the lateral surface of the cuboid for the tendon of the peroneus longus.

THE JOINTS OF THE PRIMITIVE FERUNGULATE TARSUS

In order to follow in greater detail the changes in the orientation of the tarsal joints from the primitive ferungulate to the artiodactyl type, the axes of the upper ankle joint (crurotarsal joint), the lower ankle joint (astragalocalcaneal joint), and the transverse tarsal joint will be considered separately. These axes have been located by obtaining the center of curvature of each pertinent articular surface and marking the center, where possible, on the surface of the astragalus or calcaneum. The accuracy of these determinations was tested by articulating the crural and proximal tarsal elements by wires running through these centers in such a fashion that approximately normal joint movement could be observed. While this was done with the ligaments in place in a recent artiodactyl, it was necessary to use accurately made plaster casts for the fossil form (*Claenodon*).

The upper ankle joint is located (figs. 2a, 3a) between the tibia and fibula on one side and the astragalus and calcaneum on the other. Movement at this joint in all terrestrial mammals is largely restricted to dorsiflexion and plantar flexion (extension) of the foot on the crus. Such limitation of motion probably was present in the most advanced therapsids, following the development of a trochleated astragalus and external and internal malleoli.

Although the trochlear crests are very low in the primitive ferungulates, the external and internal malleoli are well developed and probably prevented any possibility of horizontal rotation at this joint. The axis of the upper ankle joint in *Claenodon* (fig. 2A) passes from the middle of the dorsal border of the astragalocalcaneal facet to a point on the rim of the sustentacular facet of the calcaneum. This axis is thus oriented at right angles to the

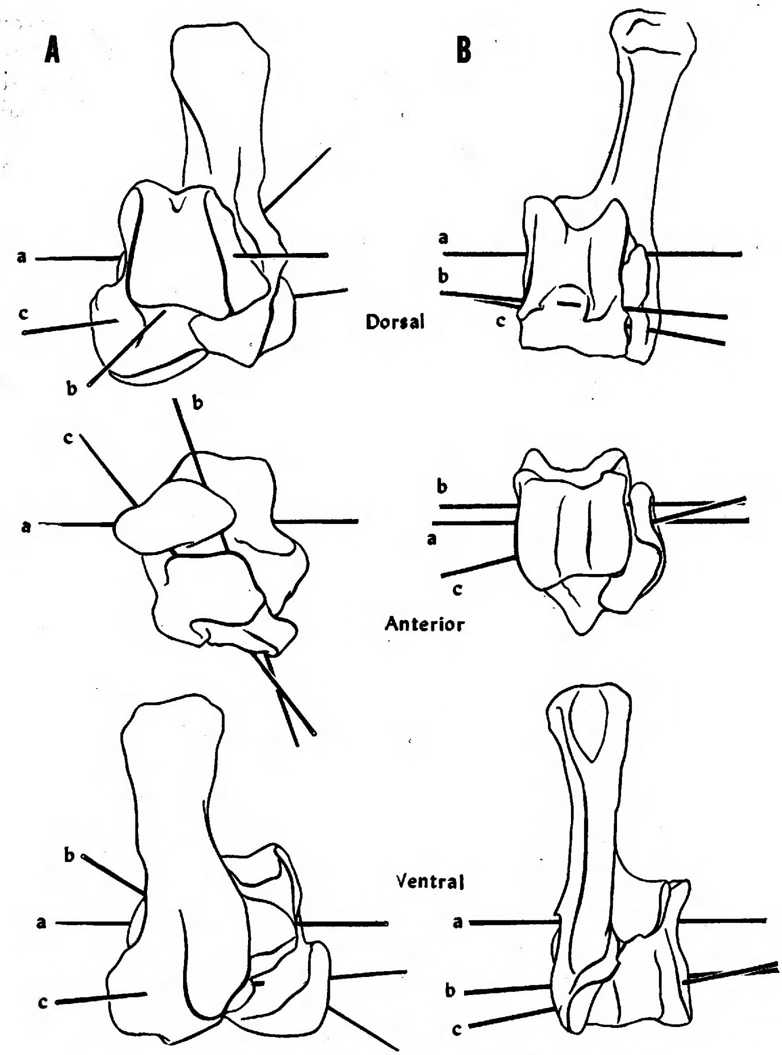

Fig. 2. The articulated astragalus and calcaneum of (A) *Claenodon* and (B) *Ovis* in dorsal, anterior, and ventral views, oriented with the axis of the upper ankle joint in the horizontal plane. *Abbreviations:* a, axis of upper ankle joint; b, axis of lower ankle joint; c, axis of transverse tarsal joint.

tibial trochlear crests as in man (Elftman and Manter, 1935) and as might be expected in a simple ginglymoid joint.

The lower ankle joint (fig. 1A, B, E) between the astragalus and calcaneum, is composed of three articulations, the astragalocalcaneal, the sustentacular, and the distal astragalar. The axis for this joint, as pointed out by Fick (1911), must be considered as a compromise axis for the articulations involved. It has a very oblique position in *Claenodon* (fig. 2A), running from a point on the middle of the dorsal surface of the neck distal to the tibial trochlea, to a point on the lateral side of the calcaneal tuber on the same level as the peroneal tubercle.

Movement at the lower ankle joint has been described by Fick and others as essentially a rotation about a compromise axis of the entire portion of the foot below the astragalus and resulting in eversion and inversion of the foot. In this connection the rounded astragalar head is of great

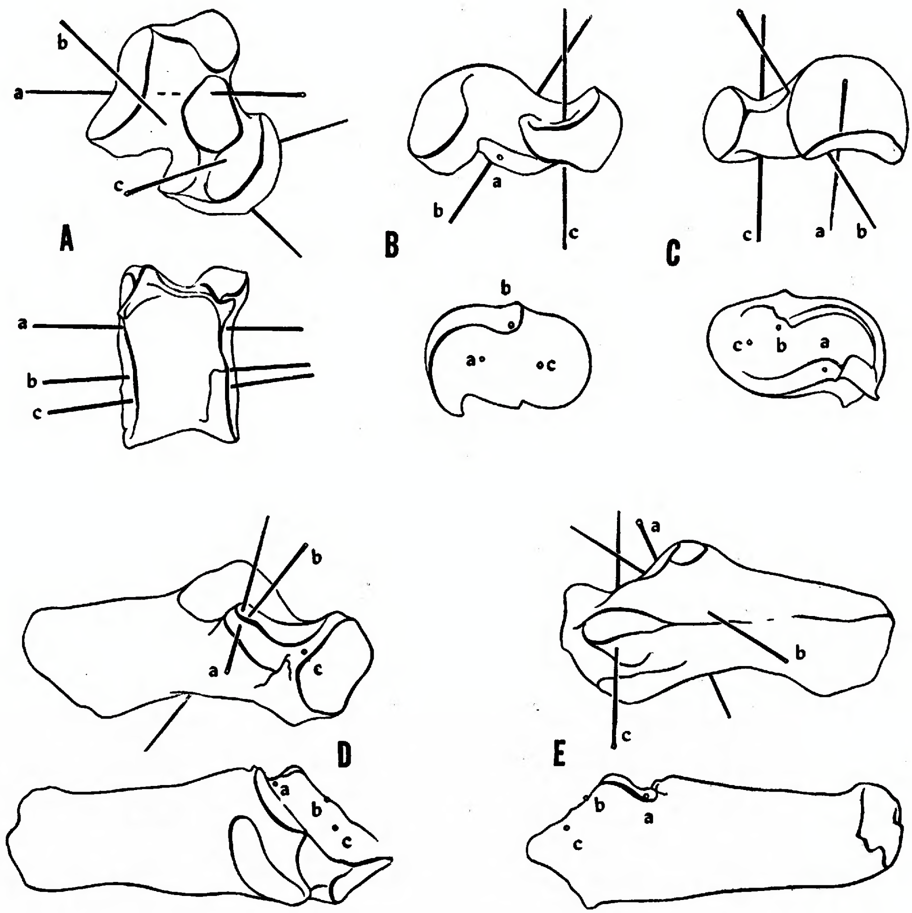

Fig. 3. A comparison of the relative positions of the axes of the three tarsal joints in *Claenodon* (upper illustration of each figure) and *Ovis* (lower illustration of each figure). A. Ventral view of astragalus. B. Medial view. C. Lateral view. D. Medial view of calcaneum. E. Lateral view. The axes indicated by circles are oriented at right angles to the plane of the figure. The positions of the axes in the calcaneum of *Ovis* represent the situation at extreme plantar flexion. Actually, the axis of the lower ankle joint is the only one bearing a constant relationship with the calcaneum during astragalar rotation. *Abbreviations:* a, upper ankle joint; b, lower ankle joint; c, transverse tarsal joint.

importance during eversion and inversion as it gives the navicular the necessary freedom of movement. The functional model of the *Claenodon* foot clearly demonstrates that such movement occurred about the compromise axis. It was important in maintaining balance through postural adjustment during locomotion.

The transverse tarsal joint is located between the astragalus and the calcaneum on the one side and the cuboid and navicular on the other. The axis of this joint is difficult to determine with accuracy in the *Claenodon* foot. Fick (1911) and Elftman and Manter (1935) differ in their opinions as to its location in man. The difficulty lies in the analysis of the movement that occurs at this joint. The studies of Weidenreich (1921) and Elftman and Manter demonstrate that in mammals with a well-defined motion at the transverse tarsal joint, the movement should be considered simply as dorsiflexion and plantar flexion rather than eversion and inversion. In man, these authors have shown that the transverse tarsal joint is normally fixed in

a dorsiflexed position, producing the longitudinal arch. In the chimpanzee and in other primates it is movable, permitting dorsiflexion and plantar flexion.

In *Claenodon*, as in most non-cursorial mammals, the astragalonavicular articulation is a saddle joint, while the calcaneocuboid articulation is ellipsoidal. As two joint articulations are again involved, a compromise axis must be determined. Sobotta and McMurrich (1914) point out that, although these articulations are primarily biaxial, they check each other in a reciprocal fashion so that during actual motion of the entire transverse tarsal joint a common uniaxial hinge joint results. The axis in *Claenodon* (fig. 2A) passes from about the midpoint on the medial face of the astragalar head to the lateral surface of the calcaneum immediately under the peroneal tubercle.

The extent of movement in the transverse tarsal joint of *Claenodon* cannot be accurately determined. The close similarity between the form of the articular surfaces in *Claenodon* and in the chimpanzee, where motion is known definitely to occur, indicates that at least a limited amount of movement was possible. Furthermore, X-rays of the canid tarsus (fig. 4A) demonstrate that very limited motion occurs at this joint during dorsiflexion and plantar flexion, foreshadowing the condition in the artiodactyls. The significance of such movement is problematical in a non-arboreal, non-grasping foot, and it might be simply a passive effect of foot action. There is no reason for believing that the transverse tarsal joint in *Claenodon* was fixed as it is in man, even though the foot was semiplantigrade (Matthew, 1937). A range of movement about equal to that in the dog probably existed.

THE PRIMITIVE ARTIODACTYL TARSUS

The dichobunid artiodactyl *Diacodexis*, from the lower Eocene Wasatchian (Gray Bull) deposits of North America, is the earliest known member of the Artiodactyla. It was small, lightly built, and presumably had five toes, although this is not certain. In any case, the tarsus completed its transformation into the artiodactyl type before there was any significant alteration in the digits by way of reduction in number or increase in relative length. This fact is of importance in considering the mechanical advantage of the tarsus in the more primitive members of the order.

The astragalus of *Diacodexis* (fig. 1C) is typically artiodactyl in all respects. The tibial trochlea is deeply grooved, and the trochlear crests are sharp. The trochlea is oriented at an angle of about 12 degrees (trochlear angle) with the long axis of the entire bone, representing a definite reduction in the size of this angle from the condition in *Claenodon*. The relationship between the position of the tibial trochlea and foot motion is obvious. The larger the trochlear angle, the greater the amount of pedal eversion in dorsiflexion, an important factor during the rapid locomotion of a long-limbed ungulate or carnivore. The tibial trochlea has often been compared to a screw mechanism, with the pitch of the screw directed outward.

The astragalar neck is recognizable only in dorsal aspect as a somewhat constricted area between the tibial trochlea and the head. The elaboration of the latter into a second trochlea resulted in an encroachment on the primitive neck area.

The astragalar head is dorsoventrally compressed to some extent, as in the primitive ferungulates. It is no longer rounded mediolaterally, however, but has sharp angular medial and lateral borders. The trochlear surface is divided into distinct cuboid and navicular facets, separated by a rather pointed crest. The navicular portion of the trochleated head curves onto the plantar surface, while the cuboidal part ends abruptly before reaching the sustentacular facet. The position of the head, with its longitudinal axis almost in line with that of the body, is undoubtedly associated with the fact that the astragalus transmits most, if not all, of the body weight directly from the tibia to the cuboid and navicular.

The distal astragalar facet is a semicircular articular surface on the lateral side of the head and is confluent with the cuboidal portion of the head. It is relatively larger than in *Claenodon* and is of greater functional importance.

The plantar surface of the artiodactyl astragalus is dominated by the sustentacular facet. It is a long narrow oval with the long axis coinciding with the long axis of the entire bone. The astragalocalcaneal facet has an outline similar to that found in *Claenodon;* its long axis, however, parallels that of the sustentacular facet. The interarticular sulcus has virtually disappeared with the loss of the interosseous ligament and the approximation of the astragalocalcaneal and sustentacular facets. The former position of the sulcus, however, can still be readily determined in most primitive artiodactyls as a very shallow groove.

The oreodont calcaneum (fig. 1F), which is very similar to the available fragmentary *Diacodexis* calcaneum, is mediolaterally compressed, particularly in the body. As in the astragalus, the long axis of the astragalocalcaneal facet is about parallel to the long axis of the entire bone and is in a more vertical position than the homologous facet in *Claenodon.* The fibular facet has essentially the same orientation. The sustentaculum is buttressed against the proximal portion of the tuber and does not project medially as a well-defined shelf as in *Claenodon.* The sustentacular facet faces distally and hence cannot function as a support for the astragalus, as pointed out by Forster (1926), but only as a guiding surface during astragalar rotation.

As a result of the compression of the body of the calcaneum, the slightly concave cuboid facet is very narrow mediolaterally. It is confluent with the distal astragalar facet that is located on the medial surface of the body.

THE JOINTS OF THE ARTIODACTYL TARSUS

The axes of the upper and lower ankle joints and the transverse tarsal joint have been determined for *Ovis* in the same manner as for *Claenodon.* The small size of the tarsus and the lack of sufficient material make it impossible to determine accurately the axes in any of the dichobunids. A detailed comparison of the tarsal elements, however, indicates that the orientation of these axes is essentially the same for all artiodactyls, including the most primitive types. Because the astragalus moves independently of the calcaneum, it is not possible to locate all the axes in relation to the calcaneum, as was done for *Claenodon.*

The axis of the upper ankle joint (figs. 2B, 3) is similar in orientation to that of *Claenodon.* It passes from the outer edge of the sustentacular facet of the astragalus to a point on the medial surface of the astragalus. The slight obliquity of this axis is due to the fact that the lateral trochlear crest of the astragalus has a greater curvature than the median. This axis in dorsal aspect is oriented at right angles to the crests of the tibial trochlea. The increase in the depth of the trochlear groove and the development of a flange or intermediate malleolus (Grant, 1940) on the anterodistal surface of the tibia which fits into this groove, along with the medial and lateral malleoli, insure limitation of movement to one plane. The articulation of the lateral malleolus (fibula) with the calcaneum further serves this purpose.

Movement of the lower ankle joint (figs. 4B, 5) in the Artiodactyla is simply a restricted rotation of the astragalus in a fore-and-aft direction. Such movement is possible because of the parallel motion at the astragalocalcaneal, sustentacular, and distal astragalar facets. For practical purposes, therefore, the functional axis of the lower ankle joint may be considered to be the axis of the sustentacular articulation, and this can be convincingly demonstrated in the working model. In other words, this axis is not a compromise axis, as it probably is in most or all other orders of mammals, but the actual pivot for all three articulations.

The axis of the lower ankle joint (figs. 2B, 3) passes through the astragalus very near its anterior surface and immediately

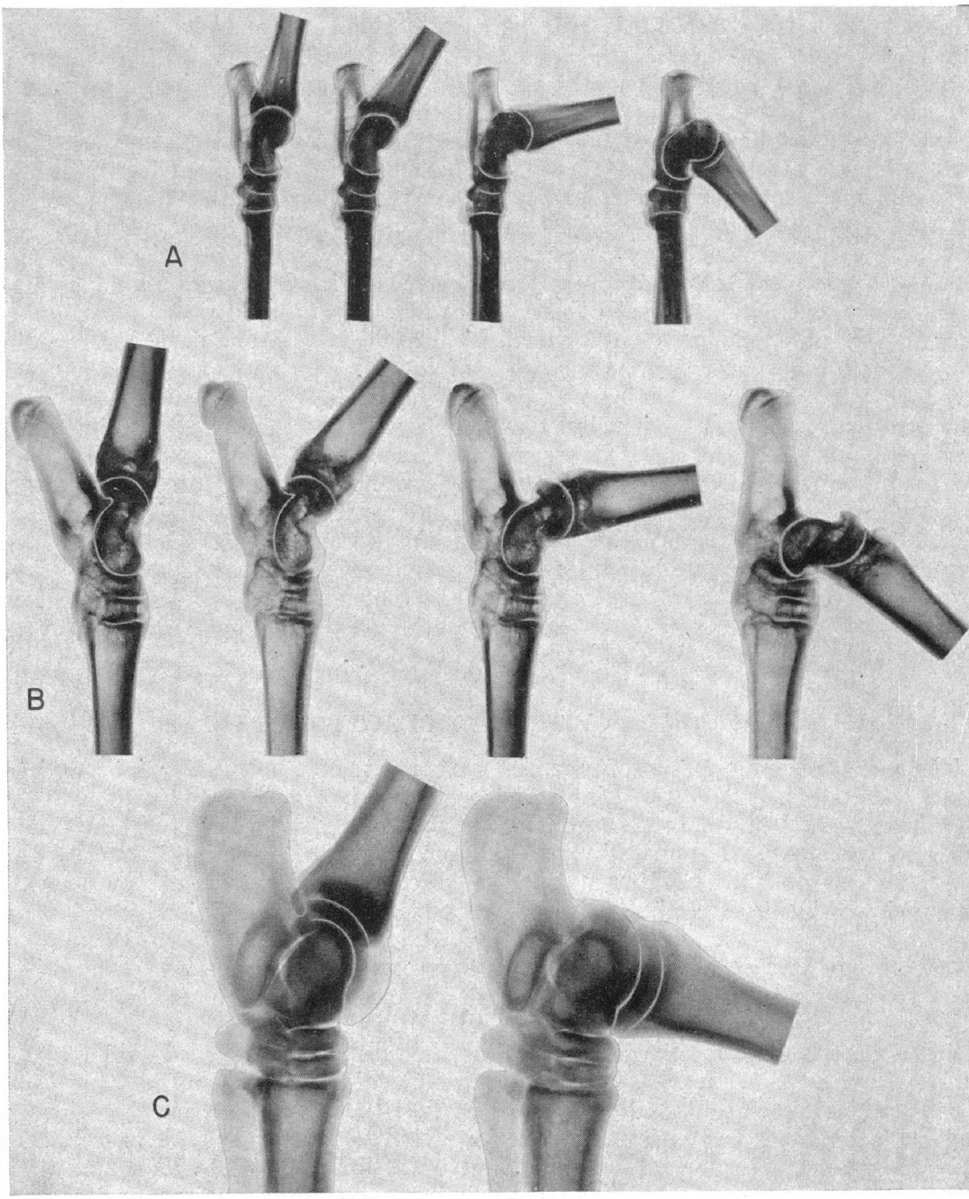

Fig. 4. Roentgenograms of the tarsus of a living dog (A), goat (B), and pony (C), showing the foot in different stages of dorsiflexion. The photographs have been oriented with the metatarsals in a vertical position.

above the border of the distal trochlea (astragalar head). This axis thus parallels that of the upper ankle joint in a modified horizontal plane and converges slightly towards it medially in a semifrontal plane. The astragalocalcaneal facet apparently lost much of its functional importance in the artiodactyls with the enlargement of the sustentacular facet and the change in the orientation of the lower ankle joint axis. While it is still present in palaeodonts, suids, ancodonts, and oreodonts, it has all but disappeared in the tylopods, tragulids, and pecorans. The

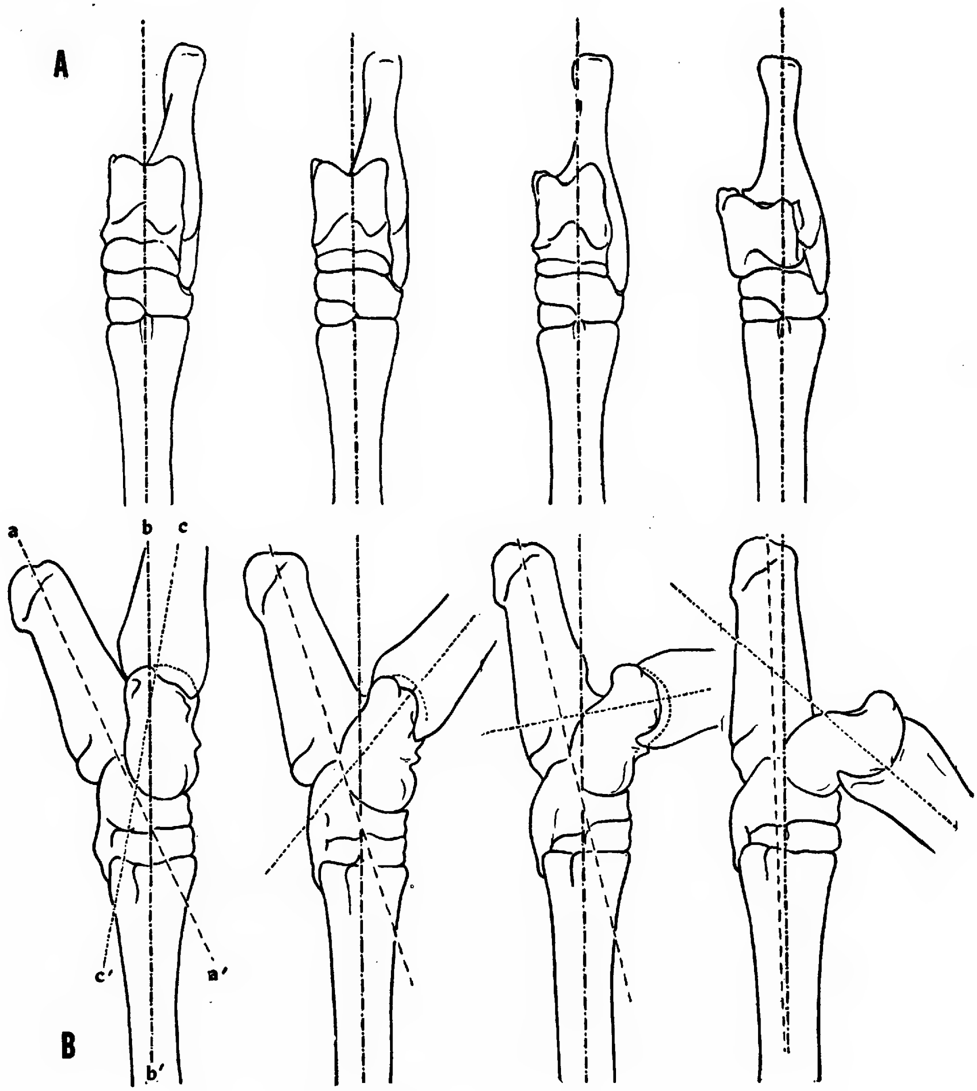

Fig. 5. Series of outlines showing the relationship between the astragalus and calcaneum during astragalar rotation. Series A (anterior view) demonstrates the movement of the calcaneum towards the midline, which is represented by the longitudinal axis of the fused metatarsals. Series B shows the movement of the calcaneal tuber into a position almost paralleling the longitudinal axis of the metatarsals. *Abbreviations:* a–a′, longitudinal axis of calcaneal tuber; b–b′, same for metatarsals; c–c′, same for tibia.

great reduction in the size and distinctness of this facet in the last three groups is the only major refinement occurring in the artiodactyl astragalus since its first known appearance in the Lower Eocene.

The action of the transverse tarsal joint (figs. 4B, 5) is limited, as in *Claenodon,* to dorsiflexion and plantar flexion of the more distal portion of the foot. Because of the presence of the trochleated astragalar head, the axis can be more readily and accurately determined than in *Claenodon* (figs. 2B, 3). It passes through the astragalus in the mid-frontal plane below the anterior dorsal border of the trochleated head. The arc of the portion articulating

with the navicular represents more than a half circle and is somewhat larger than that of the cuboidal portion, accounting for the fact that this axis converges towards the other two axes on the medial side and is diagonally placed in relation to them. The calcaneocuboid articulation has an entirely different motion that may be considered as subsidiary to the movement of the astragalus just described. During astragalar rotation, the calcaneum slides proximally or distally along the obliquely placed calcaneocuboid facets (fig. 5), the course of movement depending on the direction of astragalar rotation. It would appear, therefore, that the calcaneocuboid articulation cannot be considered as a functional part of the transverse tarsal joint but rather that movement at this articulation is a result of action at the lower ankle and transverse tarsal joints.

The orientation of the three tarsal axes clearly reflects the essential similarity of the movement occurring at the upper, lower, and transverse tarsal joints. The most radical departure from the usual mammalian condition occurs in the lower ankle joint. Eversion and inversion are no longer possible, and this movement has been translated into the comparatively simple fore-and-aft rotation of the astragalus against the calcaneum.

THE TARSAL LIGAMENTS

Ligaments are differentiated portions of the joint capsule and serve both to give stability to the joint and to restrict movement to certain more or less definite planes. As ligaments probably develop in relation to lines of tension resulting from joint function, they are presumably poorly differentiated until such function begins after birth (Clark, 1939). Elftman and Manter (1935) have pointed out that the problem of whether ligaments or muscles limit joint movement has not been settled experimentally (for instance in the maintenance of the longitudinal arch in the human foot). In ginglymoid diarthrodial joints, the ligaments are obviously of importance in preventing over-rotation and dislocation.

Camp and Smith (1942) have experimentally demonstrated the importance of the digital spring ligaments during locomotion in the horse where, through their elasticity, they play an active role in propelling the body. Most ligaments, however, such as those around the tarsus, are but slightly extensible, although the lateral and medial tarsal ligaments must be taut at all times to provide the necessary joint stability. The ligaments and the joint capsule on the anterior and posterior surfaces of the tarsus, however, are lax enough to permit the proper degree of dorsiflexion and plantar flexion.

While it has not been possible to conduct experiments on the function of the tarsal ligaments in living carnivores and ungulates, the hind limbs of a dog, horse, and deer were fixed in Klotz's fluid so as to permit manipulation of the joints and to observe the effect of the ligaments. The basic resemblance in the subdivision and arrangement of the tarsal ligaments in fissiped carnivores and artiodactyls is quite evident (fig. 6), although in the latter certain ligaments have been eliminated.

On the lateral aspect of the tarsus there are two ligaments arranged in crisscross fashion, with their fibers almost at right angles to each other. The superficial calcaneofibular ligament extends from the lateral malleolus forward to the lateral surface of the body of the calcaneum, the cuboid, and proximal portion of the lateral metatarsal. The deep calcaneofibular ligament extends in the opposite direction, from the anterior surface of the external malleolus to the proximal portion of the calcaneal tuber.

In the dog, with motion in the tarsus mostly restricted to the upper ankle joint, these ligaments are thin bands. In the artiodactyls, on the other hand, they are relatively much larger, with a tendency towards spiraling of the fibers. Here these ligaments are concerned with maintaining the integrity of the lateral side of the ankle during movement at the upper and lower

ankle joints and the transverse tarsal joint. They do not appear to be concerned with limitation of movement but rather with maintaining the proper articular relationships. The spiraling of the fibers enables the ligaments to exert a constant restraining influence by bringing the properly directed fibers into play at the proper time. The crisscross effect tends to prevent any shearing action, particularly at the upper ankle joint. The subdivision and crossing of the two parts of the calcaneofibular ligament are apparently associated with the digitigrade or unguligrade posture of the foot, positions in which the tendency towards shearing would be greater than in the plantigrade or semiplantigrade posture.

The third ligament on the lateral side is the astragalofibular ligament, extending from the posterior border of the external malleolus to the proximolateral corner of the lateral trochlear crest. Its attachment on the external mallelous being close to the axis of the upper ankle joint, this ligament remains taut throughout flexion and extension at that joint. It supplements the function of the deep calcaneofibular ligament and also, in the artiodactyls, assists in producing astragalar rotation during dorsiflexion.

On the medial surface of the tarsus the calcaneotibial ligament (part of the deltoid ligament of man) passes from the medial malleolus to the medial surface of the sustentaculum, navicular, and third cunei-

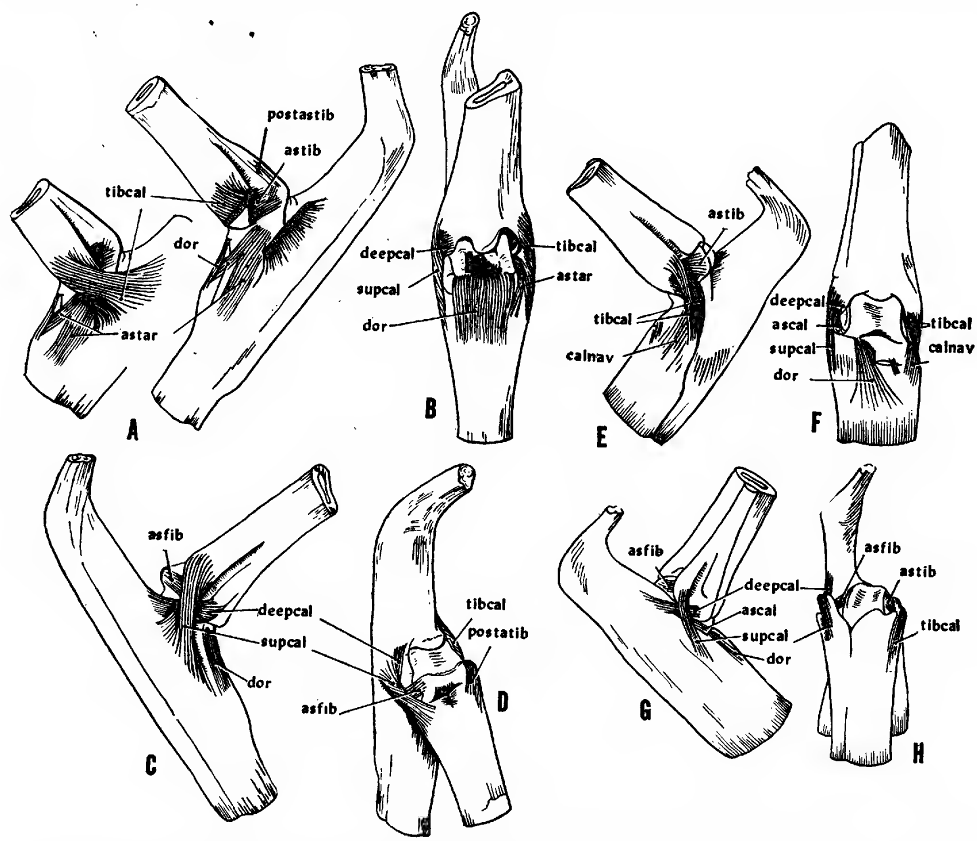

Fig. 6. The tarsal ligaments of a deer (A–D) and a dog (E–H). A, E. Medial. B, F. Anterior. C, G. Lateral. D, H. Posterior. *Abbreviations for ligaments:* ascal, astragalocalcaneal; asfib, astragalofibular; astar, astragalotarsal; astib, astragalotibial; calnav, calcaneonavicular; deepcal, deep calcaneofibular; dor, dorsal; postastib, posterior astragalotibial; supcal, superficial calcaneofibular; tibcal, calcaneotibial.

form. In the dog it is subdivided into two narrow bands, while in the pig and goat it is a single thick ligament with spirally arranged fibers. The spiraling effect serves much the same purpose as the crossed and spiraled ligaments on the lateral side of the tarsus, in that differently directed fibers become effective at different times during dorsiflexion and plantar flexion.

The calcaneofibular and calcaneotibial ligaments in the dog are concerned with maintaining the integrity of the upper ankle joint only. In the artiodactyls, they are also entrusted with the union of the lower ankle joint and the transverse tarsal joint, which accounts for their relative increase in size and complexity. These ligaments appear to have no direct relationship with the axes of the joints but rather are located in positions of greatest stress, the latter being produced by movement about the axes. They are elastic enough to maintain the proper contact at the upper and lower ankle joints during outward astragalar rotation when the space occupied by the astragalus decreases. As outward rotation progresses, they pull the calcaneum anteriorly and medially.

The astragalotibial ligament extends from the posterior surface of the medial malleolus to the medial surface of the body of the astragalus. It serves much the same function as the astragalofibular ligament.

In the artiodactyls and perissodactyls there is a strong ligament running from the medial surface of the astragalus to the lateral and dorsal surfaces of the navicular, third cuneiform, and proximal portion of the medial metatarsals. In the horse (Sisson, 1911) it is called the dorsal or oblique ligament. In the deer, however, there is a separate and distinct dorsal ligament, and the one attached to the medial surface of the astragalus will therefore be called the astragalotarsal ligament. The literature on the tarsal ligaments in carnivores indicates that the astragalotarsal ligament is absent in this group. The well-developed calcaneonavicular ligament of the dog has some fibers attached to the medial surface of the astragalus, suggesting that the astragalotarsal has been differentiated from it. The stress at the transverse tarsal joint, in the artiodactyl foot, particularly during dorsiflexion, is undoubtedly the cause for the differentiation of this ligament with its astragalar attachment. It aids in preventing dislocation at the transverse tarsal joint along with the dorsal ligament, particularly during dorsiflexion. In the horse the dorsal or oblique ligament serves the same purpose.

There is a rather well-defined ligament in the artiodactyls running from the distal posteromedial corner of the tibia to the posterior corner of the medial trochlear crest. It is closely associated with the sheath of the deep digital flexor. This ligament is here named the posterior astragalotibial ligament and it functions, along with the astragalofibular and astragalotibial ligaments, in preventing dislocation at the upper ankle joint.

The dorsal ligament of the artiodactyl tarsus extends from the anterior or dorsal surface of the astragalus to the cuboid, navicular, and, in the deer, to the proximal portion of the metatarsals. It is not so well developed in the dog, although a small triangular ligament extends from the dorsolateral portion of the astragalar neck to the cuboid and cuneiforms. The dorsal ligament is taut when the astragalus assumes a vertical position, and it assists in preventing dislocation at the transverse tarsal joint.

The joint capsule on the posterior portion of the tarsus extends from the dorsal surface of the tuber at the edge of the sustentacular facet to the posterior rim of the tibial trochlea. It is responsible, at least in part, for limiting the outward rotation of the astragalus and is taut only during the last phase of dorsiflexion.

The interosseous ligament, running between the astragalus and calcaneum in the sinus tarsi, is absent in the artiodactyls. In the dog it not only binds these two bones together, but acts as a pivot about which the inversion-eversion movement at the lower ankle joint takes place. In the perissodactyls it is relatively large and assists in preventing movement at this joint.

Although the extrinsic and intrinsic

musculature of the foot has not been particularly considered in this study, it is of equal importance in maintaining the integrity of the various tarsal joints and especially the equilibrium of the entire foot. The musculature actively participates in overcoming the effect of gravity, which, if unhindered, would cause rotatory movements at all the tarsal joints, resulting in a collapse of the foot.

THE ORIGIN OF THE ARTIODACTYL TARSUS

As the most significant changes in the development of the artiodactyl tarsus occurred in the astragalus and calcaneum, these elements have been selected for further consideration by means of the deformed coördinate method. It is of course possible, by direct comparison of these elements in *Claenodon* and a primitive artiodactyl, to visualize in a general way the transformation into the artiodactyl type. To do this in greater detail, Colbert's (1941) modification of D'Arcy Thompson's deformed coördinate method has been employed.

Briefly, the method involves superimposing, on an orthogonal projection drawing of a given part of an organism, a system of rectangular coördinates. The most primitive known stage of this part should be selected, and an aspect chosen that will show to best advantage the important changes in proportion. The coördinate system is oriented on the drawing so that the points resulting from the intersecting lines are located as nearly as possible about or in important anatomical features. On a similar aspect of the derived form, homologous points are determined as accurately as possible. These points are then connected by lines that include within the deformed coördinate system thus formed areas roughly homologous to given rectangular areas in the primitive type.

This procedure is open to several criticisms besides those discussed by Huxley (1932) which mainly apply to ontogenetic differential growth. The first, already noted by Simpson and Roe (1939), is the impossiblity of determining exactly homologous points and areas in the derived form or forms. The second is the error caused by a change in the plane or angulation of the articular facets or other important anatomical features in the descendant. This results in a foreshortening of certain areas in the projection drawing which will, of course, influence the position of the deformed coördinates. In spite of these faults, there is little question but that the method is valuable in making an analysis of the differential phylogenetic growth changes in parts of organisms that permit, by virtue of their conformation, such graphic treatment.

D'Arcy Thompson also devised a method for determining the form of a hypothetical intermediate stage between a primitive and a more specialized derived type. The validity of such a procedure is clearly demonstrated by his study of the evolution of the horse skull (Thompson, 1942). One possible objection to Thompson's method is that the more or less accurate determination of homologous points in the derived forms is apparently sacrificed in order to produce a coördinate system that shows the differential growth changes by means of uniformly curved lines. While the changes are thus indicated in a rather gross manner, the important localized deformations are usually ignored. The virtue of Colbert's modification lies in the consideration of the smaller deformations in locating the homologous points.

The determination of an intermediate coördinate system when the localized deformation is taken into account introduces additional complications. By making the assumption that all differential expansion occurred around a single arbitrarily selected point, the location of which did not change, it is then possible to superimpose the known deformed coördinate system on the rectangular with these particular points coinciding exactly and with the horizontal and vertical coördinates as nearly parallel as the deformation permits. All homologous points of the two systems are then connected by a line, and a new

point is located midway on this line. By connecting the new series of points, a third coördinate system is produced which is in virtually all respects intermediate between the other two (fig. 7D). On the system thus formed, it is possible to outline the hypothetical intermediate stage.

As has been pointed out by several authors, this method cannot elucidate any

The ventral aspect of the astragalus in *Choeroclaenus* and *Diacodexis* and the dorsal aspect of the calcaneum in *Claenodon* and *Oreodon* were selected for deformed coördinate treatment as they show the important changes in both the lower ankle joint and the transverse tarsal joint (fig. 7). The transformation thus depicted produced, as its major contribution, an as-

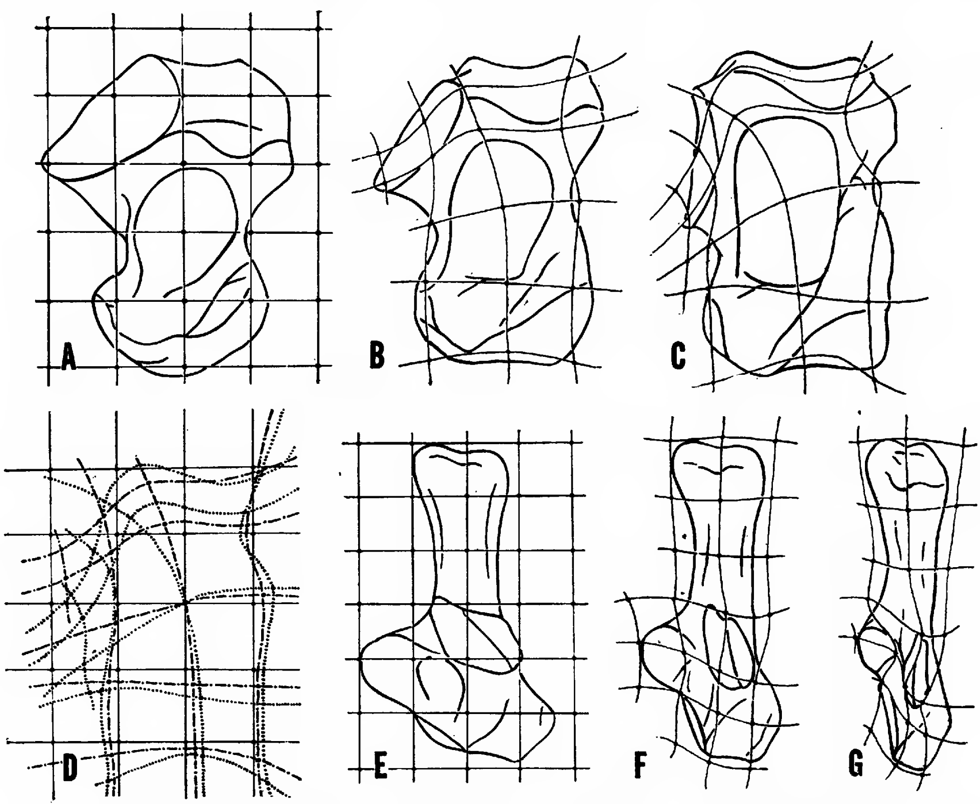

Fig. 7. Determination, by the use of the deformed coördinate method, of hypothetical intermediate stages (B, F) between the ventral aspect of the astragalus of *Choeroclaenus* (A) and *Diacodexis* (C) and the dorsal aspect of the calcaneum of *Claenodon* (E) and *Merycochoerus* (G). In D the grids of A (solid line) and C (dotted line) have been superimposed to demonstrate the method of determining the intermediate grid (dot-dash line) that forms the basis for B.

of the causative factors involved in the transformation of a primitive to a derived type, but it does present a graphic picture of the differential growth changes that probably occurred, assuming harmonious growth rates for all parts concerned. Furthermore, no claim can be made for the complete accuracy of the intermediate stage, although its similarity to an actual transitional stage is highly probable.

tragalus that is mobile only in the vertical plane.

The change in the relative size and orientation of the astragalocalcaneal facet is certainly the most obvious and probably the most radical transformation. In the astragalus, its longitudinal axis swings from a 40-degree angle with the long axis of the entire bone to one essentially parallel. As this rotation progressed, the sur-

face of the facet became directed more laterally and vertically than in the primitive ferungulates. It would appear that the approximate topographical center of this facet acted, so to speak, as a sort of pivot of differential growth, with the proximal portion of the facet swinging laterally and "pulling" the entire proximal end of the astragalus in this direction. The distal end of the facet, swinging medially, made the two sides of the astragalus more or less parallel. A similar rotation of the astragalocalcaneal facet occurred on the calcaneum, with the longitudinal axis of the facet swinging from a 45-degree angle with the long axis of the entire bone to a parallel position. The face of the facet also bebecame more vertical, in accord with the similar change in the astragalar counterpart. The fibular facet on the calcaneum underwent the same reorientation as the astragalocalcaneal.

The sustentacular facet was enlarged, changed in shape from a round to a long oval, and reoriented from a position with a decided medial tilt to an essentially right-angle one. As in the case of the astragalocalcaneal facet, the long axis of this articular surface, by the beginning of the artiodactyl stage, was alined parallel to the long axis of the astragalus. With the gradual disappearance of the interarticular sulcus, the facet expanded laterally and proximally to the ventral border of the tibial trochlea.

The marked mediolateral compression of the calcaneum in the artiodactyls was brought about largely through a migration of the sustentaculum laterally until it abutted against the proximal end of the tuber. This change occurred simultaneously with the reorientation of the astragalocalcaneal facet. The sustentacular facet became directed more distally than dorsally, a reorientation associated with the change in the posture of the foot from probably semiplantigrade to true digitigrade (as pointed out earlier, the dichobunids probably had five toes on the hind foot).

In agreement with the change in direction of the other subastragalar articulations, the distal astragalar facet was reoriented to a position almost parallel with the long axes of the astragalus and calcaneum. This was brought about with the mediolateral compression of the calcaneum. There was, in addition, a reduction in the size of the peroneal tubercle to a slight swelling, probably associated with a decrease in the functional importance of the peroneus longus as an evertor of the foot.

With the gradual alteration in the alinement of the distal astragalar facet, there was a change in the position of the axis of the lower ankle joint. In the primitive ferungulate this axis made an angle of roughly 35 degrees with the longitudinal axis of the astragalus, while in the artiodactyl it is about at a right angle to this axis. This shift in the location of the axis represents a transition from an eversion-inversion motion at the lower ankle joint to a fore-and-aft rotation. The probable location of the transverse tarsal joint axis in the hypothetical intermediate suggests a compromise between these two types of motion, and the transition from one to the other is not difficult to visualize in the functional models. The lagomorphs (Virchow, 1928) and rodents have independently developed an articulation at the lower ankle joint that permits, along with the usual inversion-eversion motion, a limited degree of vertical astragalar rotation. The astragalar head, although not trochleated, is anteroposteriorly rounded. The astragalocalcaneal facet is very large, however, and there is a strong interosseous ligament. This arrangement suggests the manner in which the functional change at this joint may have occurred with the intermediate stage represented by a compromise between an essentailly horizontal and a vertical movement of the astragalus. The lower ankle and transverse tarsal joints in certain of the Litopterna, particularly in the Proterotheriidae, also suggest a tendency towards the artiodactyl condition (Ameghino, 1905).

The development of the trochleated head on the astragalus was accomplished by a gradual "squaring off" of this area, particularly on the lateral side, thus increasing the amount of contact with the cuboid. This occurred coincidently with the nar-

rowing of the calcaneum and a reduction in the area of contact of the calcaneum with the cuboid. As stated earlier, the axis of the transverse tarsal joint probably permitted only dorsiflexion and plantar flexion in the primitive ferungulate, and that is the only motion possible in the artiodactyl. The formation of the distal astragalar trochlea and the reduction of the saddle-shaped calcaneocuboid articulation to a relatively simple sliding joint greatly increased the amount of possible movement.

There was relatively little change in the tibial trochlea of the astragalus except for a deepening of the trochlear groove, and the development of more vertical lateral and medial surfaces, resulting in a tighter articulation with the malleoli, particularly the medial one which also articulates with the calcaneum. The greater curvature of the medial trochlear crest was already present at the *Claenodon* stage and is found in most mammals.

Both Wortman (1901) and Gregory (1910) have considered the tarsus of the mesonychid creodont *Dromocyon* to be in many respects structurally ancestral to the artiodactyl type. Such a conclusion is based on the presence, in *Dromocyon*, of the deep astragalar trochlea, the oblique position of the astragalar head in relation to the body, the astragalocuboid articulation, the broadly oval sustentacular facet, and the anteroposteriorly convex navicular facet. Comparison with the hypothetical intermediate stage arrived at in this study suggests that, at best, the *Dromocyon* tarsus is representative of only a very early stage in the development of the artiodactyl type. There is, for instance, no indication in *Dromocyon* of any of the basic changes in the astragalus such as the reorientation of the astragalocalcaneal facet or of the narrowing of the body of the calcaneum.

The final result of this transformation was a different relationship between the astragalus and calcaneum. In the primitive ferungulate the astragalus rested essentially on top of the body of the calcaneum, and part of the body weight was transferred directly to the calcaneum. In the artiodactyls, with a greater elevation of the heel from the ground, the body weight is transferred directly from the astragalus to the navicular and cuboid rather than partly through the calcaneum. Coincidently with this change in weight distribution in the foot, the mediolateral compression of the calcaneal head occurred, with the final result that the calcaneum could function only as a portion of the socket in which the astragalus rotated and, of course, through the tuber as a lever arm during plantar flexion.

THE FUNCTION OF THE ARTIODACTYL TARSUS

A study of the function of the artiodactyl tarsus involves two interrelated problems, the mechanics of the tarsus itself and an evaluation of the mechanical advantage, if any, of the double-trochleated astragalus over the usual mammalian type. Unfortunately, neither question can be answered completely or conclusively until further experimental work is done on a series of living carnivores and ungulates.

The only attempt of which the writer is aware at making a mechanical analysis of the artiodactyl tarsus is that of Kripp (1935). This study centers on a discussion of the forces at work during astragalar rotation in dorsiflexion only. Kripp is of the opinion that this rotation is caused by one force acting through the calcaneum and a second force, acting in the opposite direction, through the navicular (fig. 8A). In side view, the astragalus is essentially an ellipse or, to carry the analogy further, a cam-like structure that rotates in a socket formed by the calcaneum, navicular, and cuboid. According to this concept, the axis of the cam (that of the transverse tarsal joint) being eccentrically located, a slight amount of rotation about this axis produces a measurably greater amount of movement of the proximal portion of the astragalus. On this basis, Kripp considers the independent motion of the astragalus as representing a velocity mechanism, and

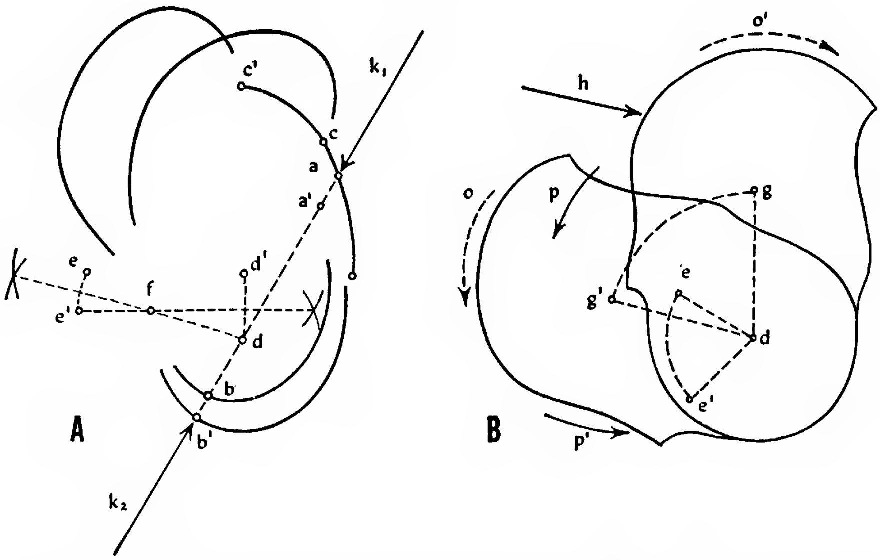

Fig. 8. A. Mechanics of astragalar rotation based on a modification of Kripp's diagram. The axis of the lower ankle joint (e) is probably not correctly located (see fig. 3b). *Abbreviations:* a–a′, displacement of calcaneum; b–b′, displacement of navicular; c–c′, extent of astragalar rotation; d–d′, displacement of axis of transverse tarsal joint; e–e′, displacement of axis of lower ankle joint; f, compromise axis of transverse tarsal and lower ankle joints; k_1, force exerted by calcaneum on astragalus at astragalocalcaneal facet; k_2, force exerted by navicular on astragalus at trochleated head. B. Rotation of the astragalus about the axis of the transverse tarsal joint (d) producing a cam-like action and resulting in a displacement of the axis of the upper ankle joint from g to g′, the velocity effect described by Kripp. While movement at the lower ankle and transverse tarsal joints occurs simultaneously, these articulations have distinct axes of rotation, and there is no evidence that a compromise axis is involved. The forces causing fore-and-aft rotation of the astragalus are primarily due to the contraction of the extrinsic extensor and flexor muscles of the foot, acting through the tibia and the ligaments running between the tibia and the astragalus. *Other abbreviations:* e–e′, displacement of lower ankle joint; h, force exerted through tibia producing astragalar rotation during plantar flexion; p and p′, forces exerted through tibia and astragalotibial plus astragalofibular ligaments producing astragalar rotation during dorsiflexion; o, direction of movement during dorsiflexion; o′, direction of movement during plantar flexion.

he concludes that this action is the functional basis for the unique structure of the artiodactyl tarsus.

Kripp's rather involved analysis of the forces producing astragalar rotation during dorsiflexion is based on the assumption that the astragalus is forced to rotate by the forward and downward movement of the calcaneum. During dorsiflexion, however, the contraction of the extrinsic extensors of the foot cannot act on the calcaneum, and presumably during this phase the flexors are relaxed. Outward astragalar rotation (clockwise when observed from the lateral side of the foot), therefore, can only be caused by, and as a result of, the dorsiflexion of the foot on the tibia. It is of course possible that a velocity effect is present during both dorsiflexion and plantar flexion.

As pointed out above, Kripp does not specifically consider the movement of the astragalus during plantar flexion (extension) of the foot, and he may have confused the forces at work during the two phases of the locomotor cycle. When the extrinsic flexors are contracting during plantar flexion, pressure is applied against the astragalus by the calcaneum, and as a consequence an equal amount of pressure is also applied in the opposite direction by the cuboid and navicular. During this phase, however, the astragalus is rotating back into its socket (counter clockwise motion when observed from the lateral side of the foot). Hence the astragalus

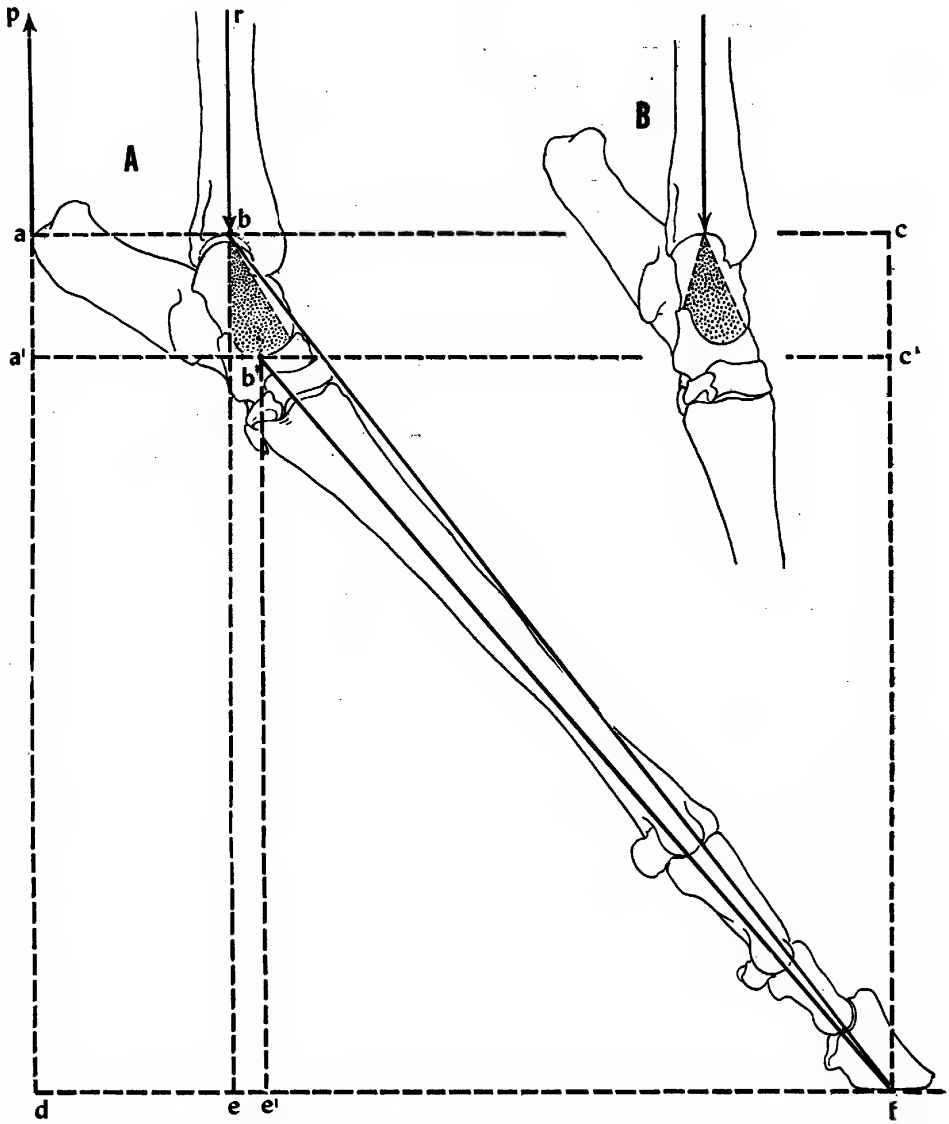

Fig. 9. A. Artiodactyl hind foot in approximate position assumed at beginning of propulsive phase of locomotor cycle. Stippled area on the astragalus represents the weight distribution in this element from the point of application of the resistance b. Details of figure explained in the text. B. Approximate position of foot at the end of the propulsive phase. Area indicating weight distribution shows virtually no change from beginning of this phase.

is moving against the forces that Kripp claims cause outward rotation and it is moving not clockwise but counterclock-wise.

Manipulation of a pig hind limb with only the skin removed demonstrates that contraction of the flexor musculature, although it brings into play the forces described by Kripp, does not inhibit the counterclockwise rotation of the astragalus. In fact, approximation of the tibia and calcaneal tuber during plantar flexion results in such a movement (fig. 5). Both the dissected specimens and the X-rays demonstrate that the movement at the transverse tarsal and lower ankle joints during plantar flexion is almost completed before that at the upper ankle joint is clearly under way.

During part of plantar flexion, before the foot hits the ground to begin the propulsive phase, the astragalus is therefore a functional part of the tibia. This situation is apparently due to the low angle of application of the crural flexors in relation to the upper ankle joint, for the tibia simply pushes against the astragalus, with the result that rotation occurs only at the transverse tarsal and the lower ankle joints (fig. 8B). By the start of the propulsive phase, an essentially right-angle relationship has been established between the calcaneal tuber and the tibia, and movement at the upper ankle joint is initiated. Hence the double-trochleated astragalus may be considered as a means of rapidly and efficiently increasing the angle of application of the crural flexor musculature when the foot is in a position of extreme dorsiflexion. This arrangement undoubtedly assists in the development of great initial propulsive power by the time the foot is in contact with the ground.

In the generalized mammalian foot, with dorsiflexion and plantar flexion restricted to the upper ankle joint, the effort and resistance moments operate about a single axis. The foot is therefore considered to be a lever of the first class during the propulsive phase (Gregory, 1912; *et al.*), and the fulcrum is represented by the contact of the tibia with the astragalus. In the artiodactyl tarsus, however, two fulcra are probably present, one (b) at the upper ankle joint and the other (b′) at the transverse tarsal joint (fig. 9). The slight amount of movement occurring at the transverse tarsal joint after the foot touches the ground is sufficient to consider this articulation as the location of a true fulcrum. By referring to figure 9, it is evident that the power component a′b′ operating about this fulcrum is greater than the component ab associated with the fulcrum at the upper ankle joint and also that the resistance component b′c′ is smaller than bc. It would appear, therefore, that at the beginning of propulsion when the resistance to continued plantar flexion is at a maximum, the optimum lever arrangement is in operation. Movement at the upper ankle joint very quickly follows, however, and the shorter power component ab becomes effective. As the foot becomes more vertical, resulting in a decrease in resistance, the power components ab and a′b′ also decrease. The contraction of the flexor musculature is, of course, of primary importance in this connection. Gray (1944) has shown that the elevation of the heel from the ground results in a decrease of the strain on the extrinsic flexor musculature. This reduction is proportional to the distance between the ankle joint and the vertical force exerted by the body. This force passes vertically through the foot in the region of the phalanges. A. Fick in 1867 pointed out that a mechanical arrangement which permits a decrease in the resistance component during muscular contraction also increases the actual work performed by that muscle. It would appear that the power component ab is the last to operate, as movement at the transverse tarsal joint apparently is concluded before that at the upper ankle joint. The exact sequence of movement at these articulations is difficult to determine, however, on the basis of available evidence.

The femorotibial and femorometatarsal indices of the more primitive artiodactyls fall within the range of the larger predatory carnivores (Gregory, 1912; Howell, 1944), although the highly cursorial artiodactyls have the highest indices among mammals. This similarity in the ratios of the primitive artiodactyls and the carnivores would place a high premium on the efficiency of the artiodactyl tarsus as a means of increasing speed or producing a great initial thrust at the beginning of the propulsive phase of the locomotor cycle. In this connection, the velocity mechanism of the astragalus would play an important role in speeding up the recovery phase and in giving the body a greater forward thrust during propulsion.

The value of the cursorial habitus in any ungulate depends largely on its functional efficiency when the animal is forced to move at high speed to escape an enemy and is, therefore, essentially a mechanism of passive defense. Laboratory tests on living artiodactyls indicate a somewhat greater range of movement in the foot than is pos-

sible in the carnivores, and there is evidence of this in Muybridge's photographs. It is probable, however, that none of the artiodactyls used in these studies were moving at their maximum rate of speed or with maximum stride, with the exception of the leaping fawn (Muybridge, 1899, p. 193) which shows very clearly extreme dorsiflexion and plantar flexion of the hind limbs. In any case, a slight increase in the range of movement plus the velocity effect during astragalar rotation and, finally, in the more advanced artiodactyls, the increased limb ratios are all factors making for greater speed and greater initial momentum during propulsion.

The perissodactyl tarsus presents a very different picture. Both manipulation of the partly dissected specimens with the ligaments *in situ* and the X-rays (fig. 4C) indicate that no appreciable movement occurs at either the lower ankle joint or the transverse tarsal joint. Dorsiflexion and plantar flexion are therefore confined to the upper ankle joint, and there is no indication that the range of motion at this joint is significantly greater than in the carnivores or artiodactyls. It would appear, therefore, that the cursorial perissodactyls such as the primitive rhinoceroses and the horses were dependent, as far as the hind limbs are concerned, upon the increased femorotibial and femorometatarsal ratios for greater speed.

Both Kripp (1935) and Howell (1944) compare the gaits in perissodactyls and artiodactyls, and this phase will not be discussed here. It should be mentioned, however, that the lightly built artiodactyls have a definite leaping stride during the fast gallop. Certain antelopes, according to Howell, may cover as much as 40 feet in a single bound. The ability to cover such a long distance in a single stride is undoubtedly associated, at least in part, with the design and function of the tarsus.

SUMMARY

1. The definitive artiodactyl tarsus as it first appears in Lower Eocene deposits represents the abrupt introduction of a basic ordinal character. There are no known intermediate or transitional stages between this tarsus and the presumed ancestral type. Predator pressure must have been an important factor in the apparent rapid evolution of this structure, which had virtually reached the biomechanical limit of specialization by the Lower Eocene.

2. Available evidence indicates that the artiodactyls evolved from the primitive hyopsodontid condylarths, although the tarsus of these early ferungulates is very similar to that of the arctocyonid creodonts. In these types, the astragalus has a shallow tibial trochlea, a wide interarticular sulcus, and a rounded head. The calcaneum has a well-developed interosseous fossa and a robust sustentaculum supporting, in part, the astragalus.

3. The axes of the upper and lower ankle joints and the transverse tarsal joint have been determined for the arctocyonid creodont *Claenodon*. These axes are oriented in several different planes, suggesting the condition occurring in the tarsus of the chimpanzee and man, which may be close to the generalized eutherian arrangement. The probable motion at each of these joints is discussed.

4. The primitive artiodactyl tarsus differs markedly from the generalized ferungulate type. The astragalus has a deep tibial trochlea, the interarticular sulcus has disappeared in connection with a reorientation of the astragalocalcaneal and sustentacular facets, and the head is trochleated. The calcaneum has lost the interosseous fossa, and the sustentaculum no longer offers direct support to the astragalus.

5. The axes of the three ankle joints have been worked out for *Ovis*. With the changes in the astragalus and calcaneum noted above, these axes are now oriented in such a manner as to permit rotation of the astragalus in a vertical plane. This motion is demonstrated in a series of X-rays of the foot of a living goat.

6. The ligaments of the artiodactyl tarsus have been modified to permit vertical astragalar rotation. The fibers of the

calcaneotibial and superficial calcaneal ligaments are somewhat spiraled in order to maintain effectively the integrity of the ankle joint during this rotation.

7. The transformation of the artiodactyl astragalus and calcaneum from the *Claenodon* type is described in detail by the use of the deformed coördinate method. The limitations of the method are discussed.

8. An attempt is made to describe the function of the artiodactyl tarsus, particularly in relation to astragalar rotation. The astragalus is essentially a cam-like structure that may be considered as a velocity mechanism. It also aids in increasing the angle of application of the crural flexor musculature at the start of the propulsive phase when two tarsal fulcra are probably present, at the upper ankle joint and the transverse tarsal joint.

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